Pollination Ecology of *Gentiana andrewsii*[1]

BARBARA H. COSTELLOE[2], Department of Biology, University of Akron, Akron, OH 44325

ABSTRACT. The pollination syndrome of *Gentiana andrewsii* Griseb., a closed, blue gentian, was investigated in a disclimax community in relation to the ecological and phenological characteristics of the surrounding plant community. *Gentiana andrewsii* is obligately dependent upon bumblebees for pollination and seed set. The flowers are self-fertile, protandrous, and herkogamous; pollen deposition is restricted to the bumblebee's sternum. Pollen is the primary bumblebee attractant; the sugar concentration of nectar is low. The corolla reflects a purplish-blue color augmented by a dissected pattern of ultraviolet light, both well-adapted to bumblebee vision. Bumblebee species show no preference among synchronously flowering species, but caste preferences are evident, with *G. andrewsii* largely attracting workers. Most local bumblebees have tongues too short to retrieve nectar from the long *Gentiana* corolla tubes; many steal nectar from lateral perforations of the corolla tube. The blooming of *G. andrewsii* at the end of the bumblebee season may have resulted from selection favoring other earlier flowering competitors. Sympatric and synchronously blooming *Gentiana crinita* Froel. (*Gentianella crinita* (Froel.) G. Don, *Gentianopsis crinita* (Froel.) Ma) also reflects the same purplish-blue color as *G. andrewsii* but with different ultraviolet reflection patterns. Nectar appears to be the primary attractant in *G. crinita*. Queens and larger workers are the most frequent visitors, tongue length being less of a discriminating factor.

OHIO J. SCI. 88 (4): 132-138, 1988

INTRODUCTION

Gentiana andrewsii Griseb., the bottle gentian, is a fall-blooming, perennial herb with closed, purplish-blue flowers. Primarily a prairie species, *G. andrewsii* is restricted to major river valleys providing moist, flat areas in early successional stages, but may have become more frequent in eastern North America owing to land clearing (Pringle 1967). It is also found in meadows, in low thickets, in wet woods, and along shores (Fernald 1950, Gleason and Cronquist 1963). Many authors have reported that *G. andrewsii* is bumblebee-pollinated (Heinrich 1979, Huxley 1888, Macior 1969), but none have elucidated its pollination syndrome or researched the effectiveness of bumblebees as pollinators of *G. andrewsii*. Indeed, there have been no studies of the pollination biology of any gentian species. The present study examines the evidence for pollination specialization of *G. andrewsii* to bumblebees, and how this species competes for pollinators in a surrounding bumblebee-pollinated plant community in northeastern Ohio.

METHODS AND MATERIALS

In September and October of 1981, 1982, and 1983, field research was conducted in a wet, deciduous, open woodland 1.6 km due north of Peninsula, Summit County, Ohio. Two adjacent stands of *Gentiana andrewsii* of about 0.2 km^2 each were studied. The first contained approximately 50 flowering plants in 1982; the second contained about 70 flowering plants. In 1983, about 130 and 230 flowering plants were studied at the first and second sites, respectively.

During the study, a total of 271 bumblebee queens, workers, and males foraging for nectar and/or pollen were collected on this and other plant species sharing these pollinators in the same area. Additionally, 177 pollinators were obtained from a preliminary unpublished study carried out in 1973 and 1974 at the same site. Behavior of bumblebees on *G. andrewsii* blossoms was recorded by visual observation in the field, both on intact blossoms and on blossoms with a "window" formed in the corolla by removing sections of petals.

Collecting was confined to favorable atmospheric conditions occurring between 0745 and 1650h, but chiefly between 1000 and 1400h when the pollinators were most abundant. A total of 147 corbicular pollen loads were obtained from bees caught during the period of 1981-1983. Pollen loads were dissociated in 70% ethanol and mounted for microscopic examination in glycerin jelly stained with methyl green. Pollen type constituents were identified, as far as possible, with reference slides of pollen collected from flowers in the research area. Pollen loads were designated as pure (i.e., pollen exclusively from the plant on which the insect was foraging), foreign (i.e., pollen exclusively from plants other than those on which the insect was foraging), or mixed (i.e., a mixture of pure and foreign pollen).

Six plants of *Gentiana andrewsii* having a total of 87 flowers were caged with fine-mesh wire screening in the 1982 season to determine fertility of flowers with bumblebees excluded. Two plants with a total of 43 flowers were left uncaged and used as controls. Of the caged plants, two were left alone; two were self-pollinated by hand; and two were cross-pollinated by hand. When flowering was complete and fruits were set, the numbers of fruits on experimental and control plants were tabulated.

Possible correlations between corolla tube depth and bumblebee tongue length were examined by measuring the corolla tube depths of 50 flowers of *Gentiana andrewsii* and 50 flowers from a nearby population of *G. crinita*, and by measuring the proboscis lengths of 59 *Bombus vagans* workers and 22 *B. impatiens* workers. Other flowers in the community were either short-tubed, nectarless, or too infrequent for measurement. Corolla tube depths were measured from the bottom of the tube, where nectar is secreted, to the point of corolla constriction where the stamens are attached and through which the bumblebee must insert its tongue (Fig. 1). Bumblebee heads were removed, soaked overnight (approx. 12 h) in a 10% solution of potassium hydroxide to soften them, and then rinsed several times in tap water. The tongues were individually extended from the heads, cut off at the base of the prementum, and mounted on slides in glycerin jelly. The lengths of the prementum plus the glossa were measured with an ocular micrometer, and the mean, range, and standard deviation of these measurements were calculated. Student's *t*-tests ($P = 0.05$) were used to determine significant differences between corolla tube depths and between bumblebee tongue lengths. Nectar depths in eight flowers of *G. andrewsii* and in four flowers of *G. crinita* were also measured using thin toothpicks of uniform size inserted into the corolla tube.

The light reflectance of *Gentiana andrewsii* and *G. crinita* corollas was measured at 30-nm intervals for 10 wavelengths (425-685 nm) on a reflecting spectrophotometer (Bausch and Lomb Spectronic 20). Reflectance percentages were plotted on Bausch and Lomb trichromatic computing forms for illuminant C and interpreted with a Maxwell color diagram. Long-wave ultraviolet reflectance (360 nm) was determined photographically with a camera equipped with a fused quartz lens mounted in an iris diaphragm with a Chance-Pilkington OX-1 ultraviolet filter. Fresh perianth parts were illuminated under artificial ultraviolet light at 360 nm by two Raytech lamps (Model LW-8L).

[1]Manuscript received 9 July 1987 and in revised form 18 March 1988 (#87-28).

[2]Present address: Dept. of Biological Sciences, Kent State Univ., Kent, OH 44242.

Nectar sugar components for *G. andrewsii* and *G. crinita* were analyzed by thin-layer chromatography using Gelman ITLC fiberglass mats impregnated with silicic acid (SA type), a developing solution consisting of 30 mL of 2-butanone, 10 mL of glacial acetic acid, 10 mL of methanol for the migrating phase, and a spray solution made of 4 g of diphenylalanine, 4 mL of aniline, 20 mL of orthophosphoric acid, and 200 mL of acetone to identify individual sugars. Nectar concentration was analyzed in six samples of *G. andrewsii* and two samples of *G. crinita*. Immediately after obtaining nectar from a flower with a micropipette, a hand refractometer was used to measure the percentage of dissolved solids expressed as sucrose equivalents.

Phenology of bloom for all plant species studied was recorded on a weekly basis in the 1982 and 1983 seasons by visual determination of peak blooming periods and bloom duration.

RESULTS

Gentiana andrewsii exhibited very low fruiting (4%, $N = 27$) when insects were excluded by caging. This may have resulted from pollination of the flower before being caged. Open-pollinated plants showed a high fruiting percentage (87%, $N = 23$); self-pollination and cross-pollination by hand showed high fruiting percentages also (100%, $N = 10$; 86%, $N = 21$; respectively). *Gentiana andrewsii* stamens and pollen invariably ripened before the stigma reached its full height in the flower and became receptive (Fig. 1, a and b).

The corolla tube of *G. andrewsii* is subcylindric, pleated, and closed at the summit (Fig. 1, a and b). In visiting the flower, a bumblebee first landed on the apex of the corolla with head and front legs directed toward the corolla lobes, and mid- and hind-legs grasping the corolla tube for support. The bumblebee then opened the corolla by manipulating the corolla lobes with its front legs and head, and crawled inside. As the bee entered the flower its sternum came in contact with the stigma of the flower, if the stigma was mature. If the bee carries pollen on its sternum from previous flower visits, pollen will be deposited on the stigma at this time. Once the bee was completely inside the flower, the corolla closed. With its head still directed downward, the bee scraped pollen from the anthers with its legs. Pollen then fell onto the sternum of the bee. The bee spent from 2 to 10 sec inside the blossom while moving around the staminal column collecting pollen. The bumblebee then backed out of the blossom, its sternum again coming into contact with the stigma if the stigma was ripe. Self-pollination is a possibility at this time if viable pollen was in the anthers. Although each *Gentiana* inflorescence contained flowers at varying stages of maturity, each bumblebee was observed to visit only one flower in an inflorescence before flying to another plant.

Of 448 bumblebees collected, 118 were taken from plants of *G. andrewsii* and 328 from plants of *Aster lateriflorus* (L.) Britt., *A. novae-angliae* L., *A. prealtus* Poir., *A. prenanthoides* Muhl., *A. simplex* Willd., *Chelone glabra* L., *Cirsium muticum* Michx., *C. vulgare* (Savi) Tenore., *Gentiana crinita* Froel., *Pedicularis lanceolata* Michx., and *Prunella vulgaris* L. Flowers of other species blooming in adjacent areas and visited periodically by these bumblebees in the same foraging trip were *Actinomeris alternifolia* (L.) DC., *Cichorium intybus* L., *Coreopsis tripteris* L., *Eupatorium perfoliatum* L., *Helenium autumnale* L., *Impatiens capensis* Nutt., *I. pallida* Nutt., *Lobelia siphilitica* L., *Mentha arvensis* L., *Pycnanthemum*

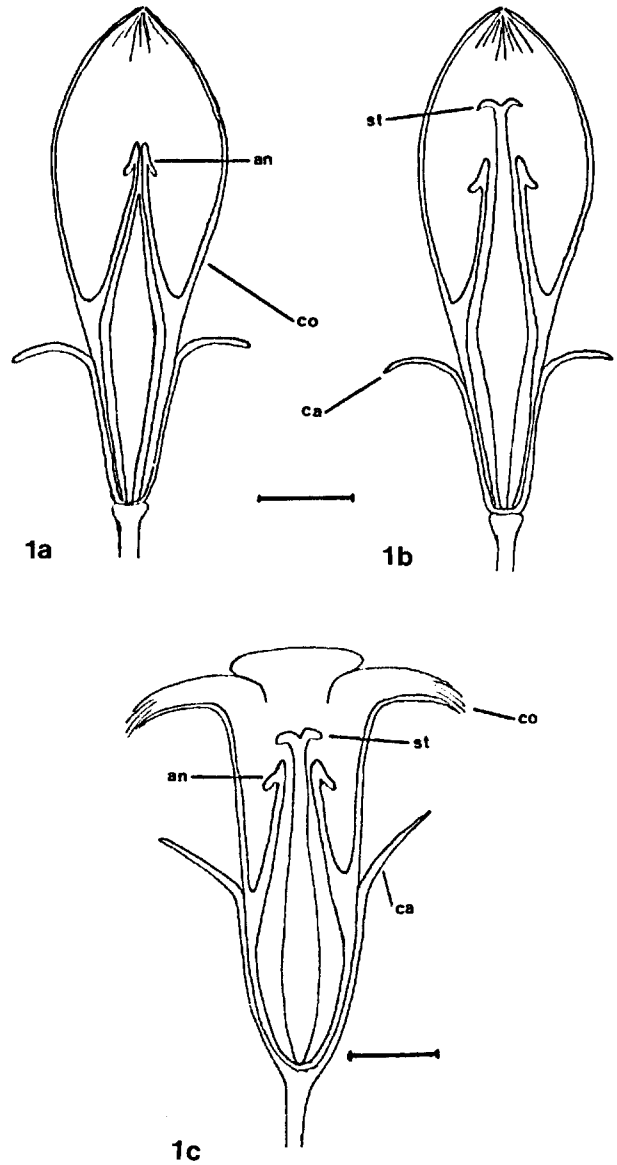

FIGURE 1. 1a, 1b — diagram of longitudinal section through *Gentiana andrewsii* flower; 1a, anthers mature; 1b, stigma mature; 1c — diagram of longitudinal section through *Gentiana crinita* flower; ca, calyx; co, corolla; an, anther; st, stigma. Bar represents 1 cm.

tenuifolium Schrad., *Solidago caesia* L., *S. graminifolia* (L.) Salisb., and *S. rugosa* Mill. The first research site, separated from the second by about 0.5 km, contained a smaller *G. andrewsii* population mixed with a greater percentage of other flower species, notably *Aster* spp., *Prunella vulgaris, Cirsium* spp., *Solidago* spp., *Pedicularis lanceolata,* and *Gentiana crinita* (only in 1982).

The dominant bumblebee species in the area were *Bombus vagans* F. Smith and *B. impatiens* Cresson (Tables 1 and 2). The data reflect no preference by any bee species for any particular plant species, except that each year a disproportionate share of *B. impatiens* visited *Pedicularis*. In addition to *Bombus* spp., three *Emphoropsis laboriosa* (two females, one male) and one *Apis mellifera* (worker) were captured inside the corolla of *G. andrewsii*.

Although there appeared to be no bumblebee species preference for plant species, the data do indicate caste preferences (Table 3). *Pedicularis* has a nectarless flower

TABLE 1

Bombus *foragers (Q = queen; W = worker; M = male) on common plant species in the* G. andrewsii *study site. Totals are for all years.*

Bumblebee species and caste		*Pedicularis lanceolata*	*Gentiana andrewsii*	*Gentiana crinita*	*Cirsium* spp.	*Aster* spp.	*Chelone glabra*	*Prunella vulgaris*	Totals
Bombus vagans	Q	0	0	1	0	0	0	0	1
	W	75	78	2	11	15	27	2	210
	M	1	3	3	2	38	0	0	47
B. impatiens	Q	0	1	0	0	0	0	0	1
	W	105	30	2	0	6	1	0	144
	M	0	1	0	1	24	1	0	27
B. affinis	W	1	0	0	0	1	0	0	2
	M	0	0	0	0	2	0	0	2
B. perplexus	M	0	0	1	0	0	0	0	1
B. fervidus	Q	0	0	1	0	0	0	0	1
	W	0	3	1	3	0	0	0	7
	M	0	1	0	1	0	0	0	2
B. americanorum	W	0	1	0	1	1	0	0	3
Totals		182	118	11	19	87	29	2	448

TABLE 2

Annual totals of bumblebees (Q = queen; W = worker; M = male) captured at G. andrewsii *study site, 1973–74, 1981–1983.*

	Years				
Bumblebee species	1973	1974	1981	1982	1983
Bombus vagans	80	26	4	83	55
(Q–W–M)	(0-79-1)	(0-25-1)	(0-4-0)	(1-45-37)	(0-48-7)
B. impatiens	49	14	0	45	64
(Q–W–M)	(1-48-0)	(0-13-1)		(0-23-22)	(0-59-5)
B. fervidus	3	3	0	2	2
(Q–W–M)	(0-3-0)	(0-3-0)		(1-1-0)	(0-0-2)
B. affinis	0	0	0	2	2
(Q–W–M)				(0-1-1)	(0-1-1)
B. americanorum	0	2	0	0	1
(Q–W–M)		(0-2-0)			(0-1-0)
B. perplexus	0	0	0	1	0
(Q–W–M)				(0-0-1)	

TABLE 3

Bumblebee caste distribution on plant species in study site (all years).

Plant species	Total (%)	Queens (%)	Workers (%)	Males (%)
Pedicularis lanceolata	41	0	49	1
Gentiana andrewsii	26	33	31	6
G. crinita	2	67	1	5
Cirsium spp.	4	0	4	5
Aster spp.	19	0	6	81
Chelone glabra	6	0	8	1
Prunella vulgaris	<1	0	<1	0

which attracted workers gathering pollen. *Gentiana andrewsii* is nectariferous and attracted mostly workers. It also attracted a few males late in the season, most of which were stealing nectar from lateral corolla perforations. The data were scanty for *G. crinita,* as bees were difficult to capture inside this flower, which, unlike *G. andrewsii,* is open at anthesis. Visual observation revealed that these flowers attracted mostly queens and larger workers, as well as a few males and smaller workers.

The various *Aster* spp. attracted a large proportion of drones. After the discovery in 1982 that asters were heavily visited by honeybees and male bumblebees, bees were no longer collected from any *Aster* species unless the bee was carrying corbicular pollen. *Cirsium* spp. attracted workers and males equally. *Chelone* plants have long-tubed nectariferous flowers and attracted mostly workers, but were sparse at the study site. *Prunella* was abundant and often visited by workers seeking nectar. These were observed to forage for pollen on *Pedicularis* in alternate visits. Because insects were difficult to capture on *Prunella,* the data do not reflect visitation frequencies.

The caste ratio of bumblebees for each week is given in Table 4; the weekly bloom phenology is shown in Figure 2. Workers predominated in the first three weeks of the study period. After the last week in Sep-

TABLE 4

Bumblebee caste ratio for each week (all years) of field study.

Week	Total bumblebees	Queens (%)	Workers (%)	Males (%)
8-14 Sep	119	0	99	1
15-21 Sep	111	0	97	3
22-28 Sep	88	1	92	7
29 Sep-5 Oct	88	2	49	49
6-12 Oct	43	2	40	58
13-19 Oct	1	0	0	100

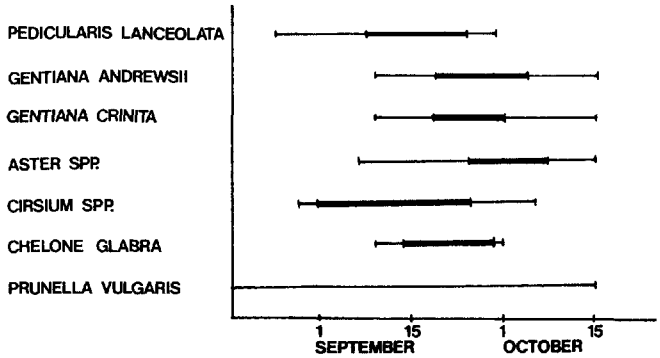

FIGURE 2. Bloom phenology. Narrow bars represent entire bloom period; wide bars represent height of bloom period.

tember, the male frequency rose sharply. The worker population was at its height during the blooming of *Pedicularis* but declined during the bloom of *G. andrewsii*. The first week of abundant bloom of *G. andrewsii* coincided with the last week of abundant *Pedicularis* bloom, at which time there were many foraging workers. Thereafter, *Gentiana* blooms saw a decline in worker population.

Of the 113 queens and workers collected on *Gentiana andrewsii* in the 1981, 1982, and 1983 seasons, 52 carried pollen loads (Table 5). Of these, 10 contained pure *G. andrewsii* pollen, 32 contained mixed pollen, and 19 contained only foreign pollen. All of the pure loads were found on bees caught at the second site, where *G. andrewsii* was by far the most abundant blossom. *Pedicularis* pollen predominated in loads from earlier in the season. At that time this flower was more abundant than *Gentiana*, and bees were only beginning to visit the latter. As *Pedicularis* abundance waned and *Gentiana* abundance increased later in the season, a higher bumblebee constancy developed for the latter as indicated by an increase of *Gentiana* pollen in corbicular loads. Pollen largely from composites but also from *Impatiens* spp., *Prunella vulgaris*, and a few unknown species was found in varying quantities and combinations in corbicular loads from bees visiting *G. andrewsii*.

Of the 77 pollen loads examined from bees visiting *Pedicularis*, over one-half were pure loads, indicating that bumblebees showed higher pollen constancies to this species than to any of the others in the community. Other pollen types found in mixed loads were mostly of the Compositae. However, *G. andrewsii* pollen was included later in the season, as well as occasional *Impatiens* or leguminous pollen.

Only three pollen loads (one each of the pure, foreign, and mixed types) were found on bees visiting *Gentiana crinita*. Other pollen species found in these loads were *Impatiens* spp., *Pedicularis lanceolata*, various composites, and a legume.

Bumblebees captured on the remaining flower species were primarily collecting nectar, as indicated by the small number of pollen loads and the predominance of foreign pollen, particularly for *Prunella*, *Chelone*, and *Gentiana crinita*. Although the primary attractant of *Aster* spp. was nectar, which particularly attracted drones, workers had a tendency to collect pollen from these flowers, especially where they occurred in abundance with other pollen-affording flowers.

Mean corolla tube depths were 14.1 ($N = 50$, SD = ± 1.08) and 13.6 ($N = 50$, SD = ± 1.67) mm for *G. andrewsii* and *G. crinita*, respectively. Mean bumblebee tongue length was 8.5 ($N = 59$, SD = ± 1.12) mm for *Bombus vagans* workers and 7.4 ($N = 22$, SD = ± 1.04) mm for *B. impatiens* workers. The difference between the corolla tube depths of the two gentian species was not significant ($P > 0.05$), but the difference between the tongue lengths of the two bumblebee species was significant ($P < 0.05$). Bumblebee tongue lengths were more than 5 mm shorter than corolla tubes with overlap in range only between *G. crinita* and *B. vagans*. The mean nectar depth of the *G. andrewsii* corolla tubes was 5.5 ($N = 8$, range = 2-9) mm; the corresponding value for the *G. crinita* corolla tubes was 3.8 ($N = 4$, range = 2-5) mm. Allowing for nectar displacement by the toothpicks used to measure depth, actual nectar depths were shallower than these values indicate and more so for the narrower *G. andrewsii*. About one-half of the bottle gentian corollas had been punctured laterally by an unknown agent just above the top of the calyx and below the staminal attachment point. Many bumblebees would steal nectar from these corolla perforations before or after visiting the same or another bottle gentian flower to obtain pollen in the legitimate manner. Earlier studies (Macior 1969) indicated that the only corolla-perforating bumblebee species inhabiting the study area is *B. affinis*. However, the piercing of gentian blossoms by any agent was not observed.

TABLE 5

Analysis of pollen types in corbicular loads. All bumblebees are of the worker caste.

Plant species	Bumblebee species	Total no. of foragers carrying pollen	Pollen load constituents		
			Pure	Mixed	Foreign
Pedicularis lanceolata	*Bombus vagans*	32	14	18	0
	B. impatiens	45	29	15	1
Gentiana andrewsii	*B. vagans*	28	6	18	4
	B. impatiens	24	4	14	6
G. crinita	*B. vagans*	1	0	0	1
	B. impatiens	2	1	1	0
Aster spp.	*B. vagans*	4	0	4	0
	B. impatiens	5	1	4	0
Prunella vulgaris	*B. vagans*	2	0	1	1
Cirsium spp.	*B. vagans*	2	0	0	2
Chelone glabra	*B. vagans*	2	0	0	2

Gentiana andrewsii nectar contained fructose and sucrose; *G. crinita* nectar contained fructose and glucose. Mean nectar sugar concentrations for the bottle gentian were 19.1 ($N = 4$, range = 16.0-21.5)% for unpunctured corollas, and 14.5 ($N = 2$, range = 11.5-17.5)% for punctured corollas. Mean nectar concentration for the unpunctured fringed gentian, *G. crinita,* was 11.8 ($N = 2$, range = 10.0-13.5)%. None of the other nectariferous blossoms in the area had enough nectar to measure with a hand refractometer.

Corollas from the two gentians had very similar color reflectance patterns. They were strongest in the violet, blue, and red ranges (Fig. 3). The color diagram composite colors were an identical purplish-blue for both species. Both species also reflected ultraviolet light, but in different patterns because the bottle gentian corolla is pleated and closed and the fringed gentian corolla is unpleated and campanulate (Fig. 4). Strong ultraviolet light reflections were also noted from the calyx of *G. andrewsii,* but not from the calyx of *G. crinita.*

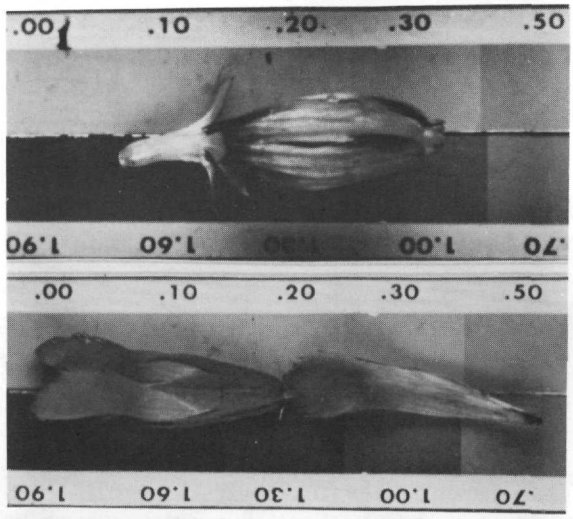

FIGURE 4. Ultraviolet corolla reflections of *Gentiana andrewsii* (a) and *G. crinita* (b). In b, entire flower is at left and adaxial side of one petal is at right. The Kodak gray scale corresponds to 40.5% UV reflectance at 0.00; 31.5% at 0.10; 19.2% at 0.20; 12.0% at 0.30; 7.0% at 0.50; 5.0% at 0.70; 3.0% at 1.00; 2.5% at 1.30; 2.0% at 1.60; and 1.5% at 1.90.

DISCUSSION

Pollination specialization to bumblebees is evidenced by several features of the flower of *Gentiana andrewsii,* which are adaptively integrated with the morphology and behavior of bumblebees. *Bombus* spp. are the only insects observed to have the strength and learning capability necessary to open the closed corolla consistently. Pollen deposition is restricted to the bee's sternum; cross-pollination occurs when the bee next visits a gentian flower with a mature stigma. Since *G. andrewsii* flowers are self-fertile, there is a limited possibility of self-pollination by bumblebees if viable pollen remains in the anthers of a flower with a mature stigma. Further research on the length of viability of pollen from this plant might help elucidate the extent to which self-pollination occurs.

Gentiana andrewsii flowers are visible to bumblebees, reflecting a purplish-blue color. This is a color shown to be easily "fixed" to and remembered by bumblebees (Heinrich 1979). Strong ultraviolet light reflections from the corolla and from the calyx enhance its attractiveness, as does the dissected pattern created by these reflections. Bees can distinguish between degrees of brokenness in patterns. It has been shown also that the more "disruptions" there are in a pattern, the more easily a bee can train to it (Michener 1974, von Frisch 1971).

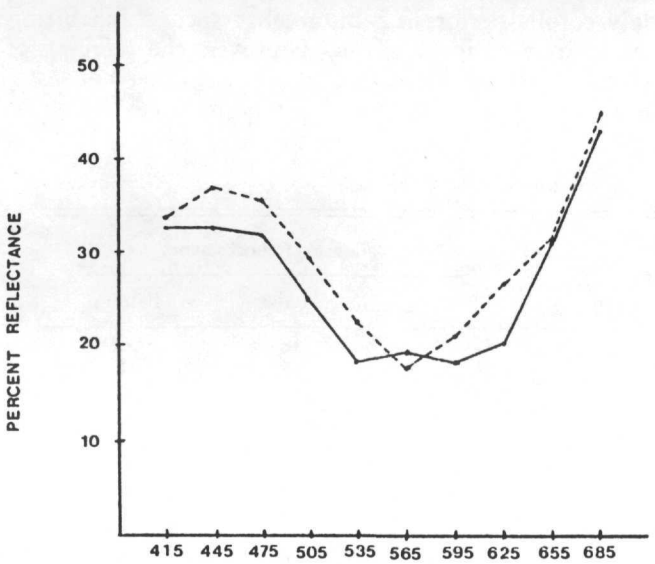

FIGURE 3. Corolla reflectance spectra of *Gentiana andrewsii* (solid line) and *G. crinita* (broken line).

Nectar concentration of *G. andrewsii* is low for attracting bumblebees according to figures given by Corbet (1978) and von Frisch (1971), but still within the range of desirability. Heinrich (1979) found that the closed gentian (no species named) contained nectar with 45% sugar. This is a greater concentration than most other bumblebee flowers. It is possible therefore that selection pressure is not great enough to sustain high nectar concentration in *G. andrewsii* (at least in this study site), as workers are the most effective pollinators and are more attracted to pollen resources. In this study, the majority of workers visiting this flower had proboscides too short to reach nectar in the long *G. andrewsii* corolla tubes and could only retrieve nectar when stealing it through lateral perforations of the corolla. Even though gathering nectar in this manner does not result in pollination, this phenomenon may not be maladaptive. Since bumblebees are not obliged to visit an alternate flower species as an energy source, the opportunity to gather nectar illegitimately could sustain forager interest in *G. andrewsii.*

In the present study, there were only two instances of bumblebee species preference for flower species. Firstly, a disproportionate share of *Bombus impatiens* visited *Pedicularis lanceolata.* In contrast, Macior (1969) found *B. vagans* to be the more common visitor to this species. This apparent preference may actually be due to annual fluctuations in local environmental conditions. Different years may see the emergence of different dominant bee species owing to the availability of preferred nesting sites or queen production the previous year. In

addition, *B. vagans* may be foraging later in the season than *B. impatiens,* because the former emerges later in the spring. Secondly, long-tongued bumblebee species (*B. fervidus, B. americanorum*) were captured foraging exclusively on plant species with long-tubed flowers (*Gentiana* spp., *Cirsium* spp.). Macior (1969) showed that *G. andrewsii* is visited by the longer-tongued *B. fervidus,* possibly in preference to the shorter-tubed, nectar-affording flowers in the area. Although *B. fervidus* visited *G. andrewsii* to the exclusion of *Pedicularis* in the present study, the paucity of *B. fervidus* precluded statistical studies comparing its frequency to shorter-tongued bumblebee species in order to show resource partitioning based on tongue length. Other studies have shown that bumblebee species coexisting in a local area tend to avoid overlap in nectar resource utilization by having different tongue lengths. This is because bumblebees have high energy demands and are able to exploit a large variety of nectar sources (Heinrich 1979). To demonstrate resource partitioning attributable to tongue-length and nectar-depth, *G. andrewsii* should be studied where it coincides in habitat with more numerous populations of longer-tongued bumblebees.

Bumblebee caste preferences were more apparent than species preferences in this study. New queens and males have no protein requirement when they emerge from the nest in autumn; their sole nutrient source at that time is nectar. Conversely, workers must gather copious amounts of pollen and nectar to provision the nest. Workers will be attracted to flower species offering abundant forage but having complicated floral mechanisms obstructing easy access to the food offered. Foragers lacking the strength or innate capability to work these mechanisms will not utilize these flowers; competition for these food resources is thereby reduced. The bee gains proficiency at a floral contrivance by repeated visits, and concurrently preserves the energy needed to learn how to work new floral devices. As a result, bumblebees will tend to remain constant to flowers with intricate mechanisms, particularly if they are abundant. Both *Pedicularis* and *G. andrewsii* attract workers with their hidden and copious pollen resources. Workers visiting *Pedicularis* forage alternately on *Prunella vulgaris* as an energy source (Macior 1969, this study). *Gentiana andrewsii* offers nectar in addition to pollen, so in certain cases (i.e., bumblebees that are longer-tongued or that steal nectar) workers may not have to seek an alternate energy source. The vast majority of the drones were found foraging on *Aster* spp. which have more easily-obtained nectar in short tubes. Previous studies corroborate this common behavior of male bumblebees, which are frequently found seeking nectar on composites (Medler and Carney 1963, Plath 1934). Although few bumblebees were captured on *G. crinita,* field observations indicated that nectar was the primary attractant. Queens and larger workers were the most frequent visitors, and pollen from the *G. crinita* flower was rarely found in corbicular loads. Tongue length may be less of a discriminating factor to visitors of *G. crinita* owing to its wider corolla when compared to that of *G. andrewsii.* This leads to the conclusion that bumblebees can force their heads past the staminal attachment point, thereby shortening the distance to the nectar.

Even though competition is keen in disclimax communities, *Gentiana andrewsii* appears to compete successfully for pollinators at this research site. Pollen constancy of bumblebees, as reflected in the number of pollen types in pollen loads, can indicate interspecific competition of plants for pollinators. At the beginning of the gentian bloom period, *Pedicularis* was the dominant blossom in the area and attracted most of the worker bumblebee population. Pollen loads reflected this dominance; constancy was high as indicated by the preponderance of pure *Pedicularis* pollen in corbicular loads. The few bees captured on *G. andrewsii* at that time also carried chiefly *Pedicularis* pollen. Since *Pedicularis* served as an abundant pollen source, few workers were interested in *G. andrewsii* at that time. Bumblebees would approach a gentian flower but, not knowing the gentian mechanism, would fly to another more familiar blossom (usually *Pedicularis*) rather than attempt to pry open the corolla. It was not until *Pedicularis* flowering began to wane that workers tried to manipulate the gentian blossoms. Pollen loads show, however, that at this early point in the gentian season, much more forage was still being gathered from *Pedicularis.* Once *Pedicularis* flowering declined and *G. andrewsii* became the more abundant pollen source, constancy of bumblebees to *G. andrewsii* became greater. Only pure pollen loads were found at the second research site, where *G. andrewsii* was the most abundant blossom even at the beginning of its bloom. All of the corbicular loads from the first site, where *G. andrewsii* was proportionately less abundant, contained mixed and foreign pollen with up to six different pollen types in a single load. Thus, bumblebees were exhibiting greater constancies toward the more numerous blossom types available. This is a common bumblebee behavior (Levin and Anderson 1970, Percival 1965, Thomson 1981). It is tempting to suggest that *G. andrewsii* may be more abundant at the second site because competition for pollinators is less severe. However, since both *G. andrewsii* populations increased greatly in size from 1982 to 1983, greater competition for pollinators at the first site probably had no detrimental effects on the reproductive success of the population. Also, even though it appeared that in the beginning of the gentian bloom period gentian flowers were not being visited by bumblebees, seed set was not detrimentally affected (i.e., the first flowers to bloom in the season yielded full seed pods).

In considering the evolution of the *G. andrewsii* pollination syndrome, it is noteworthy that the species blooms when the bumblebee worker population is declining and fewer flower species are competing for pollinators. *Gentiana andrewsii* also appears most often in disclimax communities such as the one under study here, where competition is most severe. Common responses to pollinator scarcity created by severe competition are thought to be a strengthening of floral signals in order to increase attractiveness, an evolution of nectar-rich, deep-tubed flowers preferentially visited by long-tongued pollinators, and an adjustment of flowering time (Mosquin 1971). *Gentiana andrewsii* may have evolved in these ways in response to the stiff competition encountered in disclimax communities. However, more evidence is needed to clarify the selective pressures

that this flowering species may have encountered in the past. For instance, information on the flowering times of and competitive pressures on other gentian species would provide evidence as to the divergence of flowering times of *G. andrewsii* in response to competition for pollinators. To unravel the extent to which long-tongued pollinators have influenced the evolution of deep-seated nectar in *G. andrewsii,* it would be helpful to study resource partitioning where *Gentiana* spp. occur in habitats with abundant long-tongued pollinators.

ACKNOWLEDGMENTS. The author wishes to thank Dr. L. W. Macior for his invaluable guidance and assistance throughout the entire study; J. Bender, H. Roberts, and J. Costelloe for their assistance in the field; and Dr. T. S. Cooperrider for his critical review of the manuscript. Thanks go also to J. DeWitt, J. Mariappuram, and J. Skinner for the use of additional pollinators that they collected during a preliminary study in 1973-1974.

LITERATURE CITED

Corbet, S. A. 1978 Bees and the nectar of *Echium vulgare. In*: A. J. Richards, The pollination of flowers by insects. London: Academic Press; pp. 21-30.

Fernald, M. L. 1950 Gray's manual of botany. 8th edition. New York: American Book Company.

Gleason, H. A. and A. Cronquist 1963 Manual of vascular plants of northeastern United States and adjacent Canada. Princeton, NJ: D. Van Nostrand Company.

Heinrich, B. 1979 Bumblebee economics. Cambridge, MA: Harvard Univ. Press.

Huxley, T. H. 1888 The gentians: notes and queries. Linn. J. Bot. 24: 101-124, pl. II.

Levin, D. A. and W. W. Anderson 1970 Competition for pollinators between simultaneously flowering species. Amer. Nat. 104: 455-467.

Macior, L. W. 1969 Pollination adaptation in *Pedicularis lanceolata.* Amer. J. Bot. 56: 853-859.

Medler, J. T. and D. W. Carney 1963 Bumblebees of Wisconsin. Res. Bull. #240, Univ. Wisc. Agric. Expt. Sta., Madison.

Mosquin, T. 1971 Competition for pollinators as a stimulus for the evolution of flowering time. Oikos 22: 398-402.

Percival, M. S. 1965 Floral biology. New York: Pergamon Press.

Plath, O. E. 1934 Bumblebees and their ways. New York: MacMillan Co.

Pringle, J. S. 1967 Taxonomy of *Gentiana,* section Pneumonanthe, in eastern North America. Brittonia 19: 1-32.

Thomson, J. D. 1981 Field measures of flower constancy in bumblebees. Amer. Midland Naturalist 105(2): 377-380.

von Frisch, K. 1971 Bees — their vision, chemical senses, and language. Ithaca, NY: Cornell Univ. Press.